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Benthic–pelagic coupling in the Greenland–Norwegian Sea and its effect on the geological record

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Abstract The sedimentation pattern of organic material in the Greenland–Norwegian Sea is reflected in the surface sediments, although less than 0.5% of the organic matter is buried in the sediment. Maximum fluxes and benthic responses are observed during June and/or August/September, following the pattern of export production in the pelagial zone. The annual remineralization rate on the Vøring Plateau is 3.0 g C m^{-2} a^{-1}. Freshly settled phytodetritus, as detected by chlorophyll measurements, is rapidly mixed into the sediment and decomposed. It stimulates the activity of benthic organisms, especially foraminifera. The mixing coefficient for this material is $D_b = 0.2$ cm^2 d^{-1}, which is two to three orders of magnitude higher than that estimated from radiotracer methods. The effect on the geological record, however, is likely to be small. Chlorophyll-containing particles are at first very evenly distributed on the seafloor. After partial decomposition and resuspension, a secondary redistribution of particles occurs which can result in the formation of a high accumulation area, with an up to 80-fold increase in the sedimentation rate by lateral advection. This is mainly due to physical processes, because biodeposition mediated by benthic animals increases sedimentation by only a factor of two or three.

Key words Benthic–pelagic coupling
Greenland-Norwegian Sea · Remineralization
Bioturbation · Sediment accumulation

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Introduction

The amount of particulate matter in the water of the Greenland–Norwegian Sea is strongly related to the seasonal development of planktonic organisms. Planctonic organisms show strict annual cycles in the production of particles and in the export of these to deeper water masses and the seafloor. The pattern of this flux is characterized by an early summer and an autumn peak in particulate organic matter and other constituents (Peinert et al. 1987; von Bodungen et al. 1991, this issue). The amount and general pattern of this flux is similar in areas influenced by the Norwegian Current and the East Greenland Current.

Organic particles arriving at the seafloor are the only food supply for benthic organisms, and thus they should be strictly coupled with pelagic processes. Areas with a significant food supply based on methane fluxes from seeps or other forms of chemosynthetic production seem to be of minor importance. The question arises as to whether the sedimentation pattern revealed by results from sediment traps (von Bodungen et al. this issue) is visible in surface sediments of the Greenland–Norwegian Sea and whether this has consequences for the life strategy of benthic organisms.

Pigments derived from freshly settled phytodetritus or faecal pellets (Graf 1989a; Pfannkuche 1993a) are signals which can be easily detected on the seafloor. Most of the settling organic matter, however, is rapidly remineralized (dissolved) and will not be buried to enter the geological record of surface production.

The food supply elicits a benthic production and therefore benthic organisms, in turn, produce signals which may provide a geological record of bottom water conditions. A typical example provided by benthic foraminifera is discussed by Altenbach (1992), Struck (1992) and Sarnthein and Altenbach (this issue).

The activity of benthic organisms influences the geological record in two additional ways. This is especially true for surface-derived signals which are associated with food for benthic organisms. Firstly, this material

Table 1 List of areas, cruises and stations with reference to cruise reports mentioned in the text

General area	Cruise/Leg		Year	Measurements at stations		Depth range (m)
				Chlorophyll equivalents	Remineralization	
Bear Island (BI)	[e]M	13/1	1990	405, 409, 413, 425, 499, 506	405, 409, 413, 425, 499, 506	380–2500
	[f]M	17/1	1991	384, 385, 395, 375	384, 385, 395, 375	
East Greenland Basin (OG)	[c]M	7/4	1988	537	537	3000
	[d]M	10/3	1989	628		
	[f]M	17/1	1991	444	444	
	[g]M	21/5	1992	328	328	
Fluff station (FLUFF)	[d]M	10/3	1989	625, 691	625	
Kolbeinsey Ridge (KR) (west)	[g]M	21/5	1992	331, 332	331, 332	800–950
(east)				330, 333, 335	330, 333, 335	
Lofoten Basin (LB)	[b]M	2/1	1986	78	78	3300
	[c]M	7/4	1988	536	536	
	[d]M	10/3	1989	642		
	[g]M	21/5	1992	323	323	
Vøring Plateau (VP)	[a]Pos.	119	1985	292*, 293, 294, 296, 298, 299, 300, 301, 303, 304, 306, 307, 309, 310, 311, 319, 321	304, 319	950–1450
	[b]Pos.	128	1986	244, 251, 256, 258*, 281	244, 251, 256, 258*, 281	
	[a]Pos.	137	1987	137*		
	[h]Pos.	141/2	1988	1112*		
	[b]M	2/1	1986	61*, 66, 70	61*, 66, 70	
	[c]M	7/4	1988	468*, 476, 489, 504, 519, 527, 532, 533*	468*, 476, 489, 504, 519, 533*	
	[e]M	13/1	1990	383*, 576, 596, 598	383*	
	[f]M	17/1	1991	366*	366*	
	[g]M	21/5	1992	317*	317*	

* Stations used for the annual cycle in Fig. 1.
[a] Gerlach et al. 1987; [b] Gerlach et al. 1986; [c] Hirschleber et al. 1988; [d] Zeitzschel et al. 1990; [e] Gerlach and Graf 1991; [f] Suess and Altenbach 1992; [g] Pfannkuche et al. 1993; [h] von Bodungen et al. 1988; M, RV *Meteor*; Pos., RV *Poseidon*.

may be exposed to strong mixing effects (bioturbation) which disturb the geological time slice and mix signals from many thousands of years. Secondly, an effect is provided by organisms which actively collect particles from the near-bottom water masses and pass laterally across the seafloor; a process called biodeposition. This increase of the verical flux to the seafloor may be of special importance in areas of high accumulation (Blaume 1992). The major aim of this paper is to discuss the fate of signals produced in the pelagic realm: whether they are destroyed, mixed and/or accumulated in the sediments.

Methods

Sediment samples were collected using a modified multiple corer (Barnett et al. 1984), which provides eight sediment cores in 63 cm long and 10 cm i.d. Plexiglas tubes with each deployment. Generally, only the lower half of the tubes is filled. The cores had fairly undisturbed sediment surfaces.

Data from various cruises with the RV *Poseidon* and RV *Meteor* which took place during the years 1985 to 1992 are presented (Table 1). An annual cycle for chlorophyll equivalents and remineralization rates was constructed (Fig. 1) for a central station on the Vøring Plateau (67°43′ N, 05°54′ E, 1240 m water depth) using data from different years. The cruises and stations on which this cycle are based are marked with an asterisk in Table 1. Details are also given in Table 1 for the stations on the maps for which chlorophyll equivalents and remineralization rates for organic matter (Figs. 2 and 3) are presented. For detailed positions and sampling dates, see the cruise reports cited in this table.

For the analysis of chlorophyll equivalents the top 10 cm of sediment of one core from each station was sliced into 1 cm intervals. From each slice three samples of 1 cm^3 sediment were extracted with 10 ml of acetone for the determination of chlorophyll equivalents. The samples were analysed according to the method of Jeffrey and Humphrey (1975). Thus for each station 30 analyses were carried out. For the determination of the sediment oxygen demand (SOD), a measurement of biological and chemical oxygen consumption and chemosyntetic processes, three tubes from the multiple corer were incubated in the dark in a regulated refrigerator close to the *in situ* temperature of about −0.5° C. The cores were closed by a piston equipped with a magnetic stirrer. Water was taken via a 3 mm outflow for Winkler oxygen determination according to Grasshof (1976). The incubation time was about 48

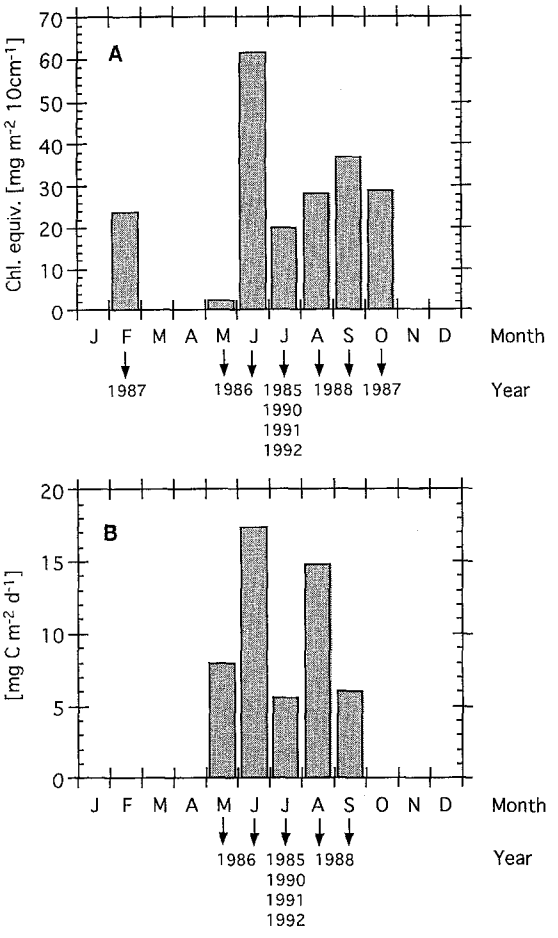

Fig. 1A, B Data for various cruises and years (1985–92, see Table 1) combined in an annual cycle of **A** chlorophyll equivalents and **B** remineralization rates for organic matter at a central station on the Vøring Plateau at 1240 m water depth. Remineralization rates were calculated from sediment oxygen demand measurements using a respiratory quotient of unity

hours. The SOD was converted into a remineralization rate using a respiratory quotient (RQ) of unity.

Results and discussion

Destruction of signals

For the central station on the Vøring Plateau, an annual cycle for the amount of chlorophyll equivalents was created by integrating values from the top 10 cm of the sediment (Fig. 1A). Although no cruise was carried out during November to January and during March and April, it is likely that chloroplastic pigments are decomposed during the winter season. The concentrations in the middle of May were zero and then dramatically increased from the end of May to June. A second peak during September corresponds to a modified export production during autumn (cf. von Bodungen et al. this issue). We have no reasonable explanation for the high concentration during February 1987. Based on chlorophyll measurements from Graf (1989a), Abele-Oescher (1991) estimated a half-life of chlorophyll in the sediments of only three to four weeks, a value that was confirmed by our shipboard incubations (unpublished data). This means that pigments settling during September at the end of the pelagic season should be completely decomposed by December. Thus the high February value indicates an unusual event and not a slow decay during the winter season.

The sedimentation pattern derived from the chlorophyll measurements differs from the results given for the seasonal flux of POC [particulate organic carbon] and PON [particulate organic nitrogen], which show a unimodel pattern with maximum fluxes during summer (cf. von Bodungen et al., Fig. 5, this issue). This variation in the shape of the sedimentation pattern can be explained by large differences in the food quality of the settling particles. Peinert et al. (1987) reported ratios of POC/chlorophyll ranging from 300 during spring to >3000 during summer. Thus the increased POC flux during summer does not necessarily mirror an increased food supply. Another indicator for food quality is the nitrogen content of settling particles. In a 1000 m sediment trap in the Norwegian Sea the flux of PON was at a maximum during August and was still high during September.

The SOD data are only available for May to September. The highest values were measured during June and August, when they were twice as high as during other seasons (Fig. 1B). This result was expected by a conceptual model given by Graf (1989b). Bearing in mind that this annual cycle is compiled from several years of data, and considering the strong interannual variabilities in the pelagic production (including a missing spring sedimentation event; von Bodungen et al. this issue), it can be stated that both the chlorophyll equivalents and the remineralization rates show a pattern similar to that derived from the sediment trap results. The highest remineralization rates coincide with the spring input and the highest PON flux occurs during late summer and autumn – that is, in contrast with the findings of von Bodungen et al. (this issue), the benthic carbon flux is determined by the export production.

Food pulses are rapidly decomposed and dominate the benthic activity for only a short period of time. In shallow waters this may be only one or two weeks (Graf 1992). In addition to this food reservoir, benthic organisms feed on older organic matter which is more difficult to digest and thus will be decomposed more slowly, producing a small background level of SOD. Because there is no seasonal temperature change in the bottom water of the Norwegian Sea, the background level will be stable throughout the year and will only be modified during periods of food pulses, when a certain amount of co-oxidation (remineralization of refractory material) may occur.

Assuming that the mean of the May and September values (7 mg C m^{-2} d^{-1}) represents this background

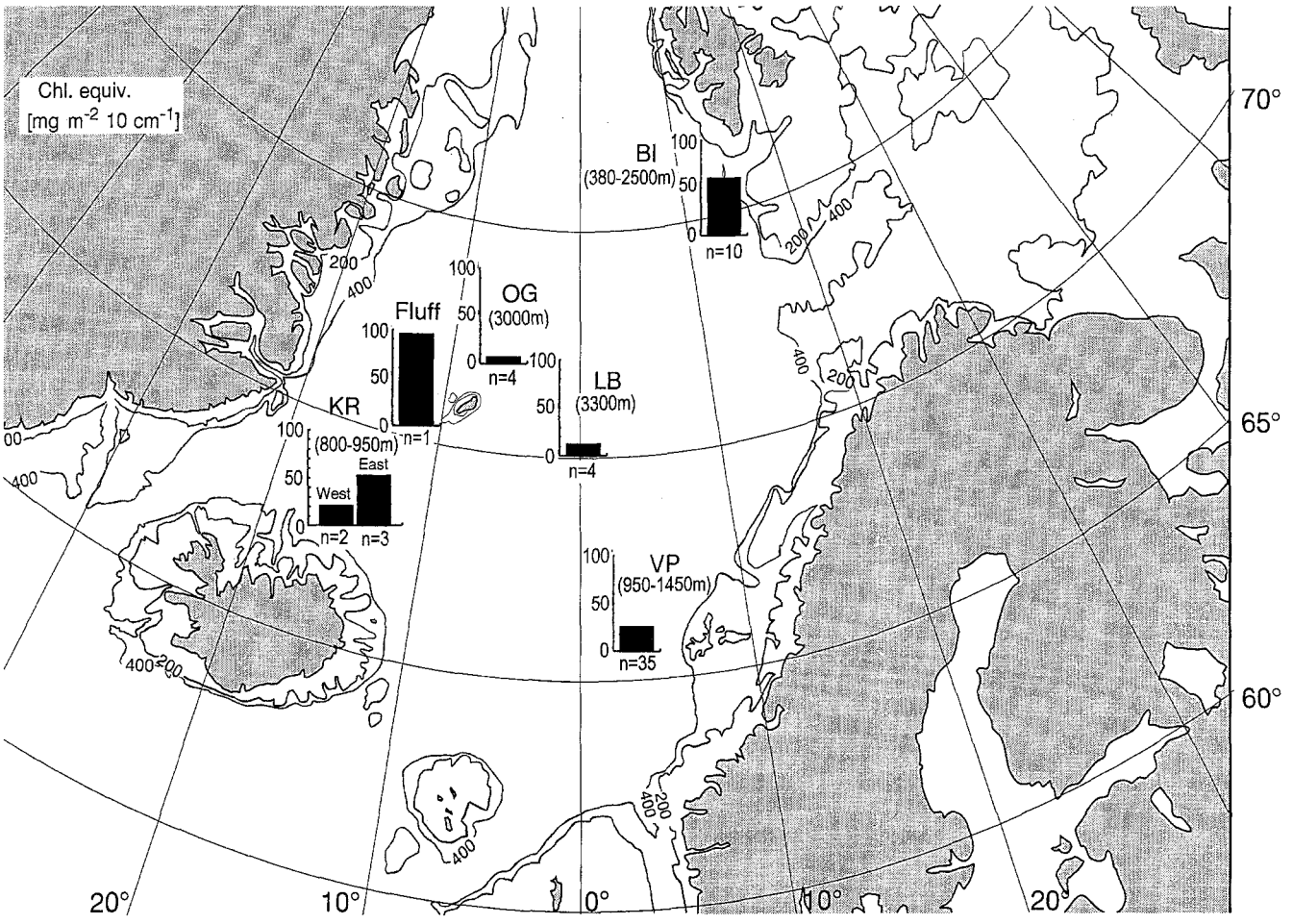

Fig. 2 Map of the Greenland–Norwegian Sea showing mean values of chlorophyll equivalents for the central working areas. VP = Vøring Plateau; KR = Kolbeinsey Ridge; FLUFF = Fluff (freshly settled detritus) station; LB = Lofoten Basin; OG = East Greenland Basin; BI = Barents Sea slope; *n* = number of stations (details in Table 1)

level, and adding the measured values for the summer months, the annual remineralization would account for about 3.0 g C m^{-2} a^{-1}. This result is in good aggreement with the annual mean of 2.2 g C m^{-2} a^{-1} calculated from three years of sediment trap deployment (von Bodungen et al. this issue) as well as with the model prediction of Suess (1980). Applying his formula for 1240 m water depth and a primary production of 90 g C m^{-2} a^{-1}, a carbon flux of 3.03 g C m^{-2} a^{-1} can be expected. The difference (0.83 g C m^{-2} a^{-1}) may be accounted for by near-bottom processes taking place in the benthic nepheloid layer (BNL) (see later).

It is obvious that the pelagically produced chlorophyll and the settling organic matter (OM) are almost completely decomposed. Therefore, a study of Recent processes can hardly relate to the small fraction of OM that is buried in the sediment. Wagner (1993) gives an accumulation rate of 0.38–0.50 g TOC m^{-2} a^{-1} for a comparable station on the Vøring Plateau. This is 10–15% of the flux to the seafloor or 0.34–0.45% of the primary pelagic production. Such results can only be achieved by measuring accumulation rates on geological time-scales.

As described by von Bodungen et al. (this issue), the same amount of primary production can result in different qualities of the settling particles. Close to the ice edge in the western part of the Norwegian–Greenland Sea a higher sedimentation rate of aggregates formed by diatoms can be expected (c.f. Grebmeyer and Barry 1991). This is visible in the sediments from the Kolbeinsey Ridge (KR) and a station south-west of Jan Mayen (FLUFF), where a fluffy phytodetritus layer of 1–2 cm thickness was observed during *Meteor* cruise M 10/3 (Fig. 2). Such layers have also been described by Billett et al. (1983) from the Porcupine Seabight and by Thiel et al. (1988/1989) from the North Atlantic (BIOTRANS area) (Hecker 1990). At these stations Heeger (1990) found the most pronounced response of foraminifera to fresh food. The food vacuoles were filled to capacity with diatoms and dinoflagellates. Linke (1992) also found the highest metabolic activity of the dominant foraminiferal species here compared with measurements from other stations in the Greenland–Norwegian Sea.

On the Barents Sea slope (BI) the lateral input of organic particles from the huge adjacent shelf area may be responsible for values of chlorophyll equivalents

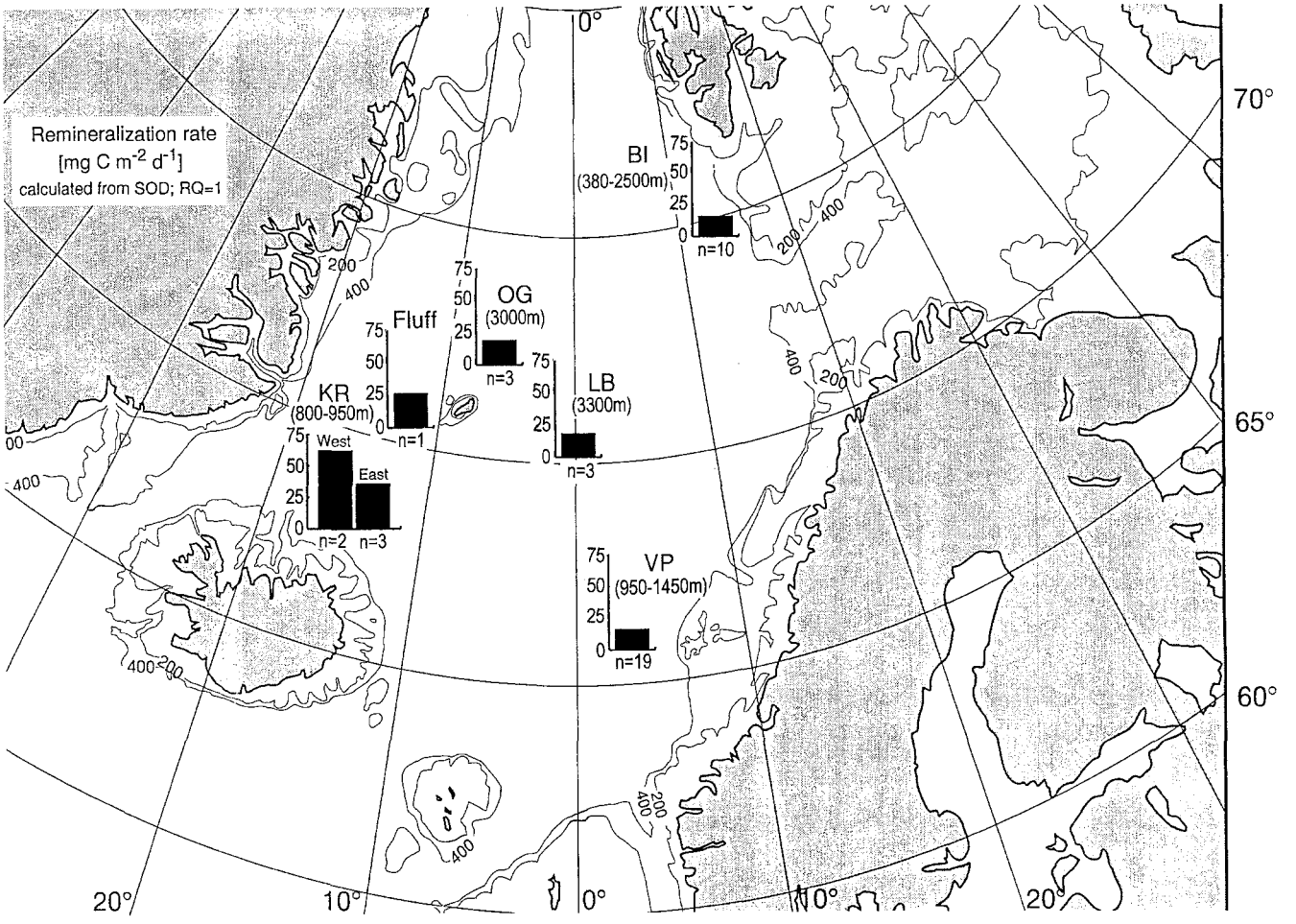

Fig. 3 Map of the Greenland–Norwegian Sea presenting mean values of carbon remineralization rates for the central working areas. Abbreviations as in Fig. 2

twice as high as those of the Vøring Plateau (see later).

In East Greenland and the Lofoten Basin (OG and LB) substantially less chlorophyll equivalents arrive at the seafloor, probably due to the greater water depth, leading to longer residence times in the water and hence increased decomposition during settlement.

For the remineralization rates (Fig. 3) the differences seem to be less pronounced, although the Kolbeinsey Ridge (KR) stations show increased values, especially the western slope. Details of this area are discussed by Brandt (1993). For the deep-sea stations (OG and LB) it has to be considered that the shipboard incubations may overestimate the SOD because of decompression effects. At depths shallower than 2000 m no significant difference was found from values obtained with an *in situ* respirometer (Pfannkuche 1993b). From these results it can be concluded that there is no constant relation between pigment flux and remineralization.

The sedimentation pattern described so far results in a special adaptation of benthic organisms to pulses of food supply. For foraminifera in particular, two different types of metabolism could be demonstrated, corresponding to an 'awakening' reaction after food input and a 'resting' or starvation metabolism during times of famine (Heeger 1990; Altenbach 1992; Graf and Linke 1992; Linke 1992). A similar result was found for bacteria (Köster et al. 1991) and for the sediment community overall (Graf 1989a).

Mixing of signals

The above-mentioned 'awakening' response of benthic organisms is not only found in the top sediment layers, but spreads down to 10 cm sediment depth within a few days (Graf 1989a). This finding was proved in shipboard experiments simulating a sedimentation event. Meyer-Reil and Köster (1992) showed the stimulation of exoenzymes which correspond to bacterial activity during the decomposition of particulate organic matter (POM). They showed enhanced activity down to several centimetres of sediment depth. These findings show a fast and deep-reaching response to sedimentation events and suggest an extremely high mixing effect on the sediment.

During the *Meteor* cruise M 10/3, with a time interval of only nine days, two multiple corers were taken at

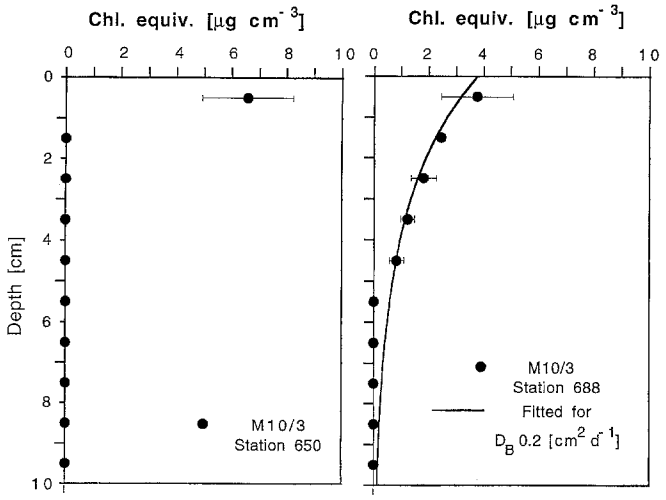

Fig. 4 Vertical profiles of chlorophyll equivalents in two sediment cores from 2530 m water depth in the East Greenland Basin. **A** Immediately after settlement and **B** nine days after settlement of fresh chlorophyll-bearing material from an ice-edge bloom on the seafloor. After nine days the chloroplastic pigments, which at first were only found in the top 1 cm of the sediment layer, were mixed down to 6 cm and the data fitted with a bioturbation model (solid line)

one position in the East Greenland Basin (650 and 688; 72°01,6N 08°34,9W) at 2530 m water depth to study the mixing effect on freshly settled chlorophyll. This food pulse just settled after an ice-edge bloom on the seafloor (Fig. 4). After nine days the chloroplastic pigments, which at first were only found in the top 1 cm sediment layer, were mixed down to 6 cm sediment depth.

To quantify this mixing effect we used a bioturbation model which was especially developed for chlorophyll (Sun et al. 1991). This model is based on Fick's second law of diffusion and assumes that the decay of chlorophyll is a first-order reaction. The latter assumption seems to be sensible because in a food-limited system the decomposition of food will entirely be dependent on the amount of available food. Thus the general equation is

$$\frac{\partial C}{\partial t} = D_b \frac{\partial^2 C}{\partial x^2} - K_d C$$

where C=chlorophyll concentration, t=time, x=sediment depth, D_b=particle mixing coefficient and K_d=degradation rate constant.

Assuming that $C=C_0$ at the sediment surface ($x=0$) and $C=C_\infty$ in $x\rightarrow\infty$, Sun et al. (1991) give a simple solution of the differential equation

$$C=(C_0-C_\infty)\exp(-x\sqrt{K_d/D_b})+C_\infty$$

In this instance the equation is further simplified because $C_\infty=0$. From the above-mentioned half-life for chlorophyll (Abele-Oeschger 1991) a degradation rate constant of $K_d=0.023\ d^{-1}$ can be calculated. The best fit with the model was achieved with a sediment mixing coefficient $D_b=0.2\ cm^2\ d^{-1}$. The modelled chlorophyll profile is given in Fig. 4B.

The model fits fairly well in the upper 6 cm of the sediment, but does not match the deeper part of the chlorophyll distribution. This reflects the fact that the modelling is based on the assumption that particle reworking can be described in analogy to diffusion. Boudreau (1986a, b) discusses this problem and distinguishes between diffusive-like mixing and non-local mixing. This means that organisms transport particles in a unidirectional way – for example, conveyer belt feeders or organism which pull particles from the surface into their burrows. According to Boudreau (1987), even the latter types of mixing would finally result in a diffusive-like profile if the process is allowed to persist long enough. In our example (Fig. 4) the process was obviously not yet completed.

In deep-sea sediments from the Greenland–Norwegian Sea only the upper 1–2 cm of sediment are sufficiently fluid that real diffusion-like mixing is possible. The depth of this layer is controlled by the activities of the epifauna and endofauna (Romero-Wetzel and Gerlach 1991). Many macrofaunal taxa are restricted to this layer; their abundance and biomass are much higher than deeper in the sediment (Romero-Wetzel and Gerlach 1991). The depth of this strongly mixed surface layer will give the maximum resolution for geological time slices, meaning that there is no possibility of differentiating between signals which were produced within the period of time which was needed to produce the time slice. In most regions of the Greenland–Norwegian Sea this will be about 1000 years. Only in high accumulation areas might there be a chance of a higher resolution.

These much higher mixing effects indicate that organisms transport particles and associated food into their burrows and probably, after digestion, also out of their burrows again. The sipunculid *Golfingia* seems to be of great importance on the Vøring Plateau. These worms are up to 80 mm long and occur with up to 90 specimens m^{-2}, comprising a biomass of up to 2 g wet weight m^{-2}. Each worm inhabits a bunch of up to 20 tiny vertical tubes (0.2–0.5 mm diameter) connected with each other below the surface, with openings at the sediment–water interface. Where populations are dense and openings numerous (up to 20000 m^{-2}), the entire sediment surface can be controlled by the 6 mm long introverts of the worms (Romero-Wetzel 1987). Obviously, *Golfingia* can transport all available organic particles from the sediment surface down, digest them within the tubes and eject faeces back to the sediment surface.

This would explain our mixing coefficient $D_b=0.2\ cm^2\ d^{-1}$, which is extremely high compared, for example, with $D_b=0.08\text{–}0.3\cdot10^{-2}\ cm^2\ d^{-1}$ derived from ^{37}Cs studies by Erlenkeuser and Balzer (1988) and other radiotracer studies (Cochran 1985).

This discrepancy clearly shows a general problem in bioturbation investigations. Smith et al. (1993) showed

that there is a strong negative correlation between the mixing coefficient D_b and the half-life of the tracer used, a phenomenon called age-dependent mixing. We think the reason for this is that bioturbation can be very selective. Organisms will mainly transport food particles. The empty test of a planktonic foraminifer may not be transported into the sediment at all. Deeper reaching transport is carried out through burrows and the food particles will be either destroyed or transported back to the surface as faecal material. Therefore, this type of mixing may have little effect on the geological record. Tracers produced in the pelagic realm will, to a large extent, end up in the Recent time slice.

A total of 70% of the total macrofaunal biomass on the Vøring Plateau is represented by large but rare species with abundances of only few specimens m^{-2}. Jensen (1992a) found up to 3.5 individuals m^{-2} of *Cerianthus* (*Anthozoa*) living in a horizontal tube 12 cm below the sediment surface. Sometimes up to 24 individuals m^{-2} of the enteropneust *Stereobalanus* live 10 cm below the sediment surface in extended horizontal galleries, connected to the surface by vertical shafts (Romero-Wetzel 1989). Although other enteropneusts are known to bring their faeces to the sediment surface, *Stereobalanus* assembles up to 1300 elongate faecal pellets at certain sites within its burrow (Jensen 1992b). Tube building is achieved by compaction of the sediment and does not result in much transport of particles. However, as long as we know so little about the feeding strategies of the very large deep-sea species, speculations are worthless. Based on *in situ* time lapse camera images, Smith et al. (1986) estimated that a population of echiurian worms in the Santa Catalina Basin mixes the top 10 cm of the sediment once in 70 years. It remains open whether this type of slow mixing or bioadvection is responsible for the low mixing coefficients found in most deep-sea environments by radiotracers, e.g. ^{210}Pb, with a long half-life (Smith et al. 1993).

Accumulation of signals

On the Vøring Plateau freshly produced pelagic material was evenly distributed in the upper sediment layers. Measurements of chlorophyll equivalents in the sediment along a north–south transect across a ridge showed a mean of 30.4 ± 3.6 mg m^{-2} and a maximum deviation of only 30% between the stations (Jensen et al. 1992). The sedimentological results, however, suggested strong differences in terms of grain size distributions and led to the recognition of an export area (with indications of erosive processes) and an import area (where sediment accumulation occurs). The latter was characterized by significantly higher amounts of clay and fine silt. The sedimentation rate in the accumulation area was 18 cm ka^{-1}, almost 18 times that of the export area.

The discrepancy between differing grain size distributions and identical chlorophyll data is probably explained by the different time-scales of sedimentation. Fresh pigment-containing material forms aggregates and hence has a fast sedimentation velocity. It reaches the seafloor within a few days (von Bodungen et al. this issue). Even if this material is resuspended by currents or animal activity, it will resettle within a distance of some ten centimeters (Lampitt 1985). A similar result was given by Thomsen et al. (1994), who deployed a special bottom water sampler providing samples from the particle gradient 5–40 cm above the seafloor. The fraction containing chloroplastic pigments is preferentially transported close to the bottom (Thomsen 1993; Thomsen and Graf, submitted) and was therefore called 'bottom heavy'. The latter term was introduced by Muschenheim (1987), who concluded from flume experiments that hydrodynamic sorting of particles occurs close to the seafloor.

Considering the activity of the abundant sipunculid (see earlier), it seems reasonable to suggest that the freshly deposited pelagic material is at first homogeneously distributed and immediately incorporated into the sediment. However, there is a permanent exchange of particles between the sediment and the benthic nepheloid layer. This process allows a secondary redistribution of already settled material. Based on ^{234}Th measurements the half-life time of particles in the benthic nepheloid layer was estimated to be in the range three to four weeks (Bacon and van der Loeff 1989). A similar result was suggested by a near-bottom sediment trap (Gardener et al. 1985). The resuspended material will be free of easily digestible organic matter, less sticky and thus transported as fine-grained material. The low settling velocity of this matter can provide a long distance lateral near-bottom transport of tenth of kilometers. For transport between resuspension and resedimentation, Thomsen (1992) calculated for particles of 3 μm diameter a distance of 25 km if they are resuspended 25 cm above the sediment and the current velocity is 10 cm s^{-1}.

In shallow waters the activity of benthic suspension feeders can significantly increase the flux of organic matter to the sediment (cf. Graf 1992; Loo and Rosenberg 1989). Whether this finding is also of importance for deep-sea stations was investigated on the Norwegian continental slope (Lutze and Altenbach 1988; Linke 1992; Linke and Lutze 1993) and has been tested on the Barents Sea slope by Thomsen (1993) and Thomsen et al. (submitted). On the Norwegian continental slope between 600 and 800 m water depth a beltlike distribution of suspension feeding benthic foraminifera occurs, extending from the Vøring Plateau northward for at least 200–300 km. Attached to hard substrates, and obviously prefering elevated positions, these specialized species are exposed to bottom currents and shifting water masses, where benthic enrichment by vertically and horizontally transported particles is thought to take place. However, the sedimentation rates are extremely low due to the high current velocities.

On the Barents Sea slope a high accumulation area was detected at about 1300–1500 m water depth corresponding, in the centre, to a Holocene sediment thickness of 8 m (Blaume 1992). The hydrographic and sedimentological details are discussed by Blaume (1992). Three deployments of the above mentioned bottom water sampler allowed a first *in situ* estimate of the impact of benthic fauna on sediment deposition. Compared with the vertical POC flux of about 20 mg C m^{-2} d^{-1} measured in a sediment trap (von Bodungen et al. this issue), biodeposition introduced an additional amount of 20–40 mg C m^{-2} d^{-1} (Thomsen 1993; Thomsen et al. submitted). The same factor of two to three was found for inorganic particulate matter.

Considering that the 'normal' Holocene sediment thickness would be only 10–20 cm, and hence the accumulation in this local deposition centre is 40–80 times higher, these results show that the Recent processes of biodeposition contribute insignificantly to the formation of the high accumulation area. At present, the high levels of sediment accumulation are believed to occur during unusual and rare events (Blaume 1992). The estimate given for the biological contribution represents no more than a first guess. We do not know whether the contribution of organisms varies within a year or is different at times of higher or lower current velocities and suspended matter supply.

On one hand, the enrichment of pelagically produced signals in high accumulation areas provides the advantage of a higher resolution of the geological record, especially if defined particles such as tests from planktonic foraminifera are sampled from the time slice of interest (Sarnthein and Altenbach, this issue). However, it is also obvious from the Barents Sea slope, where the lateral input from the shelf occurs in midwater depth (Blaume 1992), that the main portion of sediment input was transported over large distances and that signals which were produced hundreds of kilometres apart are redistributed.

Conclusions

Although the pattern of export production in the Greenland–Norwegian Sea is detectable in surface sediments, most organic tracers will be rapidly destroyed by biological degradation. Rates of burial in the sediment are low and within the uncertainties of the methods used to determine remineralization. Therefore, accumulation rates cannot be measured as recent processes, but can only be studied on geological time-scales.

The fate of a pelagically produced tracer will strongly depend on its association with food items for benthic organisms. Food uptake and bioturbation are highly selective and will produce different mixing coefficients for different tracers. The deep reaching mixing produced by animals which pull surface material into their burrows has little effect on the time slice because they tend to transport the tracers back to the surface. The top 1–2 cm are homogeneously mixed and represent the maximum resolution for time slices. The slow mixing effect of the rare, but large, species in deep-sea sediments is poorly understood. They may be responsible for mixing coefficients suggested by radiotracer methods, which are appropriate for the evaluation of the mixing effect on the geological record.

A concentration of tracers in high accumulation areas provides a chance for higher resolutions of the time slices. Benthic fauna contribute a factor of two to three, which is extremely important for benthic carbon fluxes, but less relevant for the formation of the deposition center itself. The advantage of an increased thickness of time slices in such areas is counteracted by the problem of long distance lateral transport. It will be extremely difficult to find quantitative transfer functions for these areas.

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